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High-resolution GPS tracking reveals habitat selection and the potential for long-distance seed dispersal by Madagascan flying foxes *Pteropus rufus*

Ryszard Oleksy [a], Paul A. Racey [b], Gareth Jones [a,*]

[a] School of Life Sciences, Life Sciences Building, University of Bristol, 24 Tyndall Avenue, Bristol BS8 1TQ, UK

[b] Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Cornwall Campus, TR10 9FE, UK

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ABSTRACT

Long-distance seed dispersal can be important for the regeneration of forested habitats, especially in regions where deforestation has been severe. Old World fruit bats (Pteropodidae) have considerable potential for long-distance seed dispersal. We studied the movement patterns and feeding behaviour of the endemic Madagascan flying fox *Pteropus rufus*, in Berenty Reserve, southeast Madagascar. Between July and September 2012 (the dry season) nine males and six females were tagged with customised GPS loggers which recorded fixes every 2.5 min between 18.00 and 06.00 h. The combined home range of all of the tagged bats during 86 nights exceeded 58,000 ha. Females had larger home ranges and core foraging areas and foraged over longer distances (average 28.1 km; median 26.7 km) than males (average 15.4 km; median 9.5 km). Because the study was conducted during the gestation period, the increased energy requirements of females may explain their greater mean foraging area. Compositional analysis revealed that bats show strong preferences for overgrown sisal (*Agave sisalana*) plantations (a mix of shrub, trees and sisal plants) and remnant riverside forest patches. Sisal nectar and pollen were abundant food sources during the tracking period and this probably contributed to the selective use of overgrown sisal plantations. The bats also ate large quantities of figs (*Ficus grevei*) during the study, and dispersed seeds of this important pioneer species. The bats flew at an average speed of 9.13 m/s, perhaps to optimise gliding performance. The study confirms that *P. rufus* has the potential to be a long-distance seed disperser, and is able to fly over a large area, often crossing cleared parts of its habitat. It potentially plays an important role in the regeneration of threatened forest habitats in this biodiversity hotspot.

1. Introduction

The determination of home range plays a key role in determining the potential of frugivorous animals to disperse seeds over long distances, potentially an important trait for forest regeneration. The study of home range is fundamental in conservation biology and wildlife management (Bonaccorso et al., 2002). Home range as defined by Burt (1943) is 'the area, usually around a home site, over which the animal normally travels in search of food'. It is therefore the area within which animals perform their usual activities. Home ranges may be affected by sex, age, reproductive status, hierarchy or time of

* Corresponding author.
E-mail address: gareth.jones@bristol.ac.uk (G. Jones).

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year. The migratory path is not considered as a part of the home range (Burt, 1943). In this study we describe the movement ecology of a large Old World fruit bat, the Madagascan flying fox *Pteropus rufus*, to evaluate its importance for dispersing seeds over large spatial scales in the landscape.

Pteropus species are tree-roosting and, like other bats, spend most of their lives in roosts (MacKinnon et al., 2003). Bats in this genus have the potential to disperse seeds over large distances, especially when the bat densities exceed a threshold level (McConkey and Drake, 2006). Pteropodid bats are also threatened by overhunting over much of their range, and this may reduce population size and affect the efficacy of the bats as effective seed dispersers (McConkey et al., 2012). However the distances that pteropodid bats travel for foraging (and hence their potential as long-distance seed dispersers) remain poorly documented. Individual bats may be forced to travel longer distances when in larger colonies to obtain enough food (Borkin and Parsons, 2011). Additionally, seasonal changes in the distribution and abundance of food may change quantitative and qualitative aspects of bats' foraging behaviour (Fleming and Heithaus, 1986). Several studies have been carried out to investigate foraging patterns, home range, movements and roost selection in Old World fruit bats (Pteropodidae), for example in Australia (Tidemann and Nelson, 2004; Roberts et al., 2012); Oceania (Banack and Grant, 2002; Bonaccorso et al., 2002); Africa (Jenkins et al., 2007; Kofoky et al., 2007; Richter and Cumming, 2008; Sapir et al., 2014) and Asia (Epstein et al., 2009; Tsoar et al., 2011). However, little information is available on the habitat requirements and preferences for most species in the genus *Pteropus* (Vardon et al., 2001), despite many pteropodid bat species being threatened or endangered (Mickleburgh et al., 2002). Additionally, generalising range and habitat use for *Pteropus* species could prove misleading because 86% of pteropodid species inhabit islands (Jones et al., 2009), and island species usually differ in ecology from their continental counterparts (Banack, 1998). Hence it is important to collect information about each species for conservation purposes.

Nevertheless, it is difficult to collect behavioural data from individual animals by direct observation mostly because bats' foraging activities occur between dusk and dawn and are usually out of an observer's sight (McConnell et al., 1999). Satellite transmitters have revolutionised previous technology by making it possible to track wildlife over vast spatial and temporal scales (e.g. Cyr and Nebel, 2013, Hay and Nebel, 2012, Jouventin and Weimerskirch, 1990, Richter and Cumming, 2008, Roberts et al., 2012). However, infrequent fix intervals and relatively high levels of inaccuracy (Wilson et al., 2002) are not useful for studying foraging and movement patterns at a fine scale (Ryan et al., 2004; Schofield et al., 2007). Therefore, Global Positioning System (GPS) methods have proved to be very useful for wildlife tracking. GPS tags collect data on animal positions at high rates and over short intervals (as often as every second) and have coverage over 24 h in any weather conditions, allowing tracking in remote and poorly accessible areas (Recio et al., 2011). GPS methods can also be highly accurate (typically $+/-20$ m spatial accuracy) and can store huge amounts of data that then can be transferred remotely to an operator (Tomkiewicz et al., 2010; Urbano et al., 2010). GPS methods are therefore very powerful for the study of fine-scale animal movements and foraging patterns and provide an excellent method for assessing movement ecology and the potential for long-distance seed dispersal by flying foxes.

In this study we focused on the largest endemic Madagascan pteropodid *Pteropus rufus* Geoffroy (also known as the Malagasy fruit bat). Its population size was estimated over a decade ago at 300,000 (MacKinnon et al., 2003). The current population is likely to be lower, due to hunting (Oleksy et al., 2015), and recent surveys suggest that 40% of the roosts in Mackinnon's (2003) study may no longer be present (Oleksy, 2014). *Pteropus rufus* roosts in large trees, often near rivers and in mangroves. Roosts range in size from 10 to 5000 individuals, however large roosts are now rare (probably because of habitat loss and overhunting), and the median size is 400 (Garbutt, 2007; MacKinnon et al., 2003). Sexual activity begins between April and May and young (singletons normally and twins very occasionally) are born in October and November (Garbutt, 2007; MacKinnon et al., 2003). The species is categorised as 'Vulnerable' on the IUCN Red List with a decreasing population trend, based on the loss of over 30% of its population over the last 20 years (IUCN, 2013). We aimed to determine (1) home range sizes of *Pteropus rufus*; (2) their movement and feeding patterns; (3) the distances and speed they travel at night; (4) their habitat selection and preferences. We tested the hypothesis that *P. rufus* has the potential to be a long-distance seed disperser able to cross cleared and degraded areas. If this is the case, then conservation of *P. rufus* may be important for the regeneration of forested habitats in Madagascar that have disappeared at alarming rates in recent times (Bollen and Donati, 2006; Gade, 1996).

2. Study site

The study took place in Berenty Private Reserve (25° 00′33″S; 46° 1′29″E) between July and October 2012. Berenty contains an established *P. rufus* roost containing about 600 bats at the time of the study. According to Long and Racey (2007) the roost varied in size from 500–600 individuals during the middle of the wet season (January–February) to 1800–2000 individuals at the end of the dry season (August–September) and it is one of the largest in Madagascar (Long and Racey, 2007).

Berenty Estate is located approximately 85 km west of Taolagnaro and 25 km north of the Indian Ocean (Long and Racey, 2007). It protects 200 ha of gallery forest beside the Mandrare River. Berenty, along with the Bealoka Reserve (100 ha, also part of the estate) is the largest of four gallery forests along the Mandrare River (Jolly et al., 2006). The Berenty area is arid and dominated by spiny forest vegetation that is characteristic of the southern domain of Madagascar (Jolly et al., 2006). The annual rainfall is between 400–600 mm and the temperature ranges between 25–35 ° C (O'Connor, 1987). Most rain falls between October and March (wet season) and temperatures are lowest during the dry season (April–September, 10 ° C) (Long and Racey, 2007).

Table 1
Description of all captured and tagged *Pteropus rufus* bats in Berenty Reserve. Female (p) represents pregnant females.

Date of tag attachment	Tag ID	Last date tracked	Nights of data	Sex	Reproductive status	Body mass (g)	Forearm length (cm)
23/07/2012	2407	08/08/2012	16	Male	Adult	1100	18
01/08/2012	2412	06/08/2012	5	Female	Adult	700	16
06/08/2012	24091	14/08/2012	8	Male	Immature	760	16.5
06/08/2012	2406	10/08/2012	4	Male	Adult	750	16
06/08/2012	2414	11/08/2012	5	Female	Adult	650	16
09/08/2012	24081	15/08/2012	6	Male	Immature	650	15
09/08/2012	2413	18/08/2012	9	Male	Immature	650	16
12/08/2012	2410	24/08/2012	12	Female(p)	Adult	810	18
12/08/2012	24111	15/08/2012	3	Male	Adult	800	17
14/08/2012	24051	23/08/2012	8	Female(p)	Adult	710	17
23/08/2012	24112	27/08/2012	4	Male	Immature	650	15
23/08/2012	24052	26/08/2012	3	Male	Immature	600	16
30/08/2012	24082	06/09/2012	7	Male	Adult	800	17
30/08/2012	24113	03/09/2012	4	Female	Immature	750	16
30/08/2012	24053	Lost	0	Male	Adult	900	19
03/09/2012	24092	10/09/2012	7	Female	Adult	700	16
Total nights			101				
Total excluding 1st night			86				
Mean			**6.73**			**748.89**	**16.53**
SD			**3.58**			**125.51**	**1.14**
Median			**6**			**730**	**16**
IQR			**4**			**153**	**1**

Berenty is surrounded by ca. 30,000 ha of commercial sisal plantations (*Agave sisalana*) established between the late 1930s and early 1940s. These plantations are scattered with small parcels of endemic spiny forest, which were left to act as windbreaks to protect sisal or to preserve traditional sacred sites for the local people (Long and Racey, 2007). The remaining gallery forest fragments outside the reserve are highly degraded from over-grazing by cattle (zebu) and wood extraction by local villagers (Long and Racey, 2007).

3. Methods

Between 23rd July 2012 and 3rd September 2012, 16 bats were tagged with E-obs GPS devices (GPS–ACC-Logger-Tag, e-obs GmbH digital telemetry, Munich, Germany, ca. 26 g) to monitor their movements at night. The tags were programmed to be active between 18.00 and 06.00 h. Fixes were recorded every 2.5 min when the bat was moving and every 30 min when the bat was stationary. This sampling rate was selected to provide precise information about movements and foraging sites, while still allowing a battery life of up to two weeks. Location data were stored on the tag and downloaded remotely using a hand held base-station every day between 13.00 and 14.40 h. Only within this time window was the built-in radio-transmitter on the tags programmed to emit a radio frequency, allowing location of the tag via a directional high-gain antenna (e-obs) for data downloading.

The bats were captured during their breeding season, which made it easier to assess their reproductive status (Table 1). The reproductive status of males was assessed from their body mass and external examination of the scrotal testes (Racey, 2009). Large body mass (>700 g) and large, conspicuous testes indicated an adult male. Bats with lower body mass usually had small testes indicating immaturity. Only one male bat (ID. 24091; Table 1) had a mass greater than 700 g and also possessed small testes: it was classed as an immature on the basis of testes size.

The reproductive status of females was assessed by examining their nipples. Bats with very small nipples, showing no evidence of previous suckling were classed as nulliparous and immature (Heideman, 1988). Once a female had suckled young, the nipples become dark keratinised protuberances, indicating sexual maturity and adulthood (Racey, 2009).

Early pregnancy in bats is difficult to assess (Racey, 2009). Only two females (ID. 2410 and 24051; Table 1) had obvious signs of pregnancy i.e. a swollen abdomen indicating the presence of a foetus. The rest were either in an early stage of pregnancy (which could not be diagnosed) or were sexually immature. However, nipples of nulliparous females may remain small until pregnancy is well advanced (Racey, 2009). That makes pregnancy difficult to diagnose based on nipple morphology alone.

3.1. Bat netting and tag attachment

The bats were captured using a handmade nylon net (5 m × 2 m; 10 cm mesh). The net was supported by poles and positioned at the top of sisal inflorescences during the bats' feeding time, between 18.00 and 01.00 h, in sisal plantations near the Berenty Reserve (ca. 3 km from the roost) and in the canopy of *Ficus grevei* trees in the gallery forest, ca. 1.5 km from the roosting site of the bats. After capture, each bat was weighed (2 kg Salter Spring Balance Scale; 10 g accuracy)

Table 2
Habitat types, area and their percentage occurrence within the colony's home range and individual home ranges.

Habitat code	Habitat type	Total area (ha)	Total area (%)	Mean availability within the individual home ranges (% ± SD)
1	Gallery forest	332	0.57	8.79 ± 14.94
2	Degraded gallery forest	740	1.27	2.39 ± 2.31
3	Sisal plantation (managed)	13 345	22.82	45.44 ± 24.21
4	Mixed forest	975	1.67	1.45 ± 1.36
5	Spiny forest	23 377	39.97	13.49 ± 11.98
6	Agricultural land (maize, manioc, sweet potatoes)	10 179	17.4	13.03 ± 10.81
7	Rice paddies	717	1.23	0.77 ± 1.48
8	Fruit trees (trees growing within agricultural land)	392	0.67	0.70 ± 0.60
9	Overgrown sisal (with trees and shrubs)	97	0.17	0.05 ± 0.13
10	Water bodies	2 028	3.47	6.36 ± 4.62
11	Human settlement	410	0.7	0.53 ± 0.44
12	Open areas	263	0.45	2.24 ± 2.23
13	Degraded spiny forest	5 628	9.62	4.86 ± 6.54
Total		**58 483**	**100**	

and forearm length measured (measuring tape; 0.5 cm accuracy). In order to attach the tag, a strip of fur (ca.6 cm × 2 cm) was shaved from between the animal's shoulders and non-irritant skin-bonding latex glue (Ostomy Adhesive Solution, Salts Healthcare, UK, Product code: 833005) was applied to both the skin and the tag. Only bats weighing 600 g and over were tagged in order to ensure the tag did not exceed 5% of their body mass (Aldridge and Brigham, 1988). After the glue started to dry, the tag was applied and held down for around 5 min. Once the glue had set, the bat was released at the place of capture. The glue did not provide a permanent attachment ensuring the tag would eventually fall from the animal. All procedures were authorised via ethical review at the University of Bristol's Animal Services Unit.

At the end of this study, three working tags were used to establish the accuracy and precision of the fixes. The tags were attached firmly to a leafless tree for three nights to acquire constant fixes. Distances from the attachment point and recorded fixes were then measured in Google Earth and the mean distance and variation among fixes was calculated.

4. Analysis

Ranges 7 software (Antrack Ltd, Wareham, UK; South and Kenward, 2006) was used to analyse all the data on home range size, core area size and overlap of home ranges. The GPS fixes collected during roosting/socialising were excluded from the analysis.

First, 100% minimum convex polygons (MCPs) were constructed to determine home ranges for each individual bat and for all bats tracked from the colony. The software also measured the area of the created polygons. The MCP is an example of link distance methods that assume uniform use of space within the range enclosed by the outermost locations (White and Garrott, 1990; Kenward, 2001; Kernohan et al., 2001). Second, to define core foraging areas of the bats, the analysis of utilisation distribution discontinuities were used. The utilisation distribution plots the polygon against the percentage inclusion of locations (Van Winkle, 1975). Identification of a discontinuity in this plot indicates the point where outlying fixes are excluded (Harris et al., 1990; Kenward, 1985, 1987). That allows the creation of cluster cores that indicate foraging areas. Although several methods are available to define core foraging areas of animals (Calhoun and Casby, 1958; Jennrich and Turner, 1969; Worton, 1989), cluster polygons (cores) (Kenward, 1987) seemed to be the most appropriate minimum-linkage estimators to use in the present study because bats often spent the majority of time in relatively small areas, moving quickly between them (Davidson-Watts et al., 2006).

Additionally, because home-range size increases with sampling effort before typically reaching an asymptote (Seaman et al., 1999; Powell, 2000), a plot of cumulative daily home range area against the number of tracking days was created for bats with four or more days of data to determine if home range reached an asymptotic value over the time bats were tracked.

To investigate habitat preferences of the bats, the habitat within the whole range of the tracked colony was mapped and classified into 13 categories (Table 2) using the built-in base map (Bing Map Aerial) in ArcGIS 10. The area was partially ground-truthed during fieldwork to enable recognition of different habitats on the map. Some areas could not be ground-truthed because of on-going conflict and hence risks to the safety of field workers. The ground-truthing that was conducted suggested that the mapping used was largely reliable. We also viewed the bats' trajectories in Google Earth maps that were updated recently, and spanned 2003–2013, so changes in land use could be taken into account. We are confident that our habitat descriptions were robust.

Habitat preferences of the bats were established by comparing the composition of the habitat in each bat's home range (100% MCP) with the habitat used during foraging (cluster cores of all the foraging records) using compositional analysis (Compositional Analysis Plus Microsoft Excel tool 6.2, Smith Ecology Ltd, UK) in accordance with the methods of Aebischer et al. (1993). The analysis does not take into account the proximity of a habitat to the roost and assumes that all resources are accessible. However, it highlights whether the available habitat was used randomly (i.e. in proportion to its availability) or whether bats selected specific habitats. It also ranks the habitat types according to bats' preferences and weights these in

relation to the number of fixes collected from each bat. All statistics, matrices and rank order were automatically generated by the software.

For each bat, the distances travelled at night were measured. An independent sample *t*-test with unequal variances was used to investigate whether there was a difference in an average nightly distances travelled by male and female bats. The same test was used to investigate the difference in size of home ranges (100% MCP) and core foraging areas (cluster core) between male and female bats. However, in these cases the data were transformed to natural logarithms to obtain normal distributions. The reproductive status of bats was not considered in the analysis.

The average speed of bats' flight was calculated using the GPS tracks in Google Earth. The distance travelled between at least four continuous fixes at relatively equal distances was divided by the time taken to travel the distance. Only tracks that were relatively straight (i.e. no more than 10° divergence from a straight line) and at equal intervals (i.e. fix taken every 2.5 min) were measured.

Pennycuick's model (Flight v1.24 available at http://www.bio.bristol.ac.uk/people/pennycuick.htm and described in detail in Pennycuick, 2008) was used to calculate minimum power flight speed (V_{mp}) at which the bats should fly to minimise power expenditure (hence maximum endurance) and maximum range flight speed (V_{mr}) at which bat would achieve maximum flight range for a given amount of energy. The values for *P. rufus* were calculated using average body mass of the studied bats (Table 1) and also wing span (1.22 m) and wing area (0.238 m^2) taken from Norberg et al. (2000). We acknowledge that the use of wing morphology from the captured bats would have been more appropriate, but these measurements were not made, as we wanted to return the bats to the wild as soon as possible after tagging.

5. Results

In total, 101 nights of data were collected from 15 bats (nine males and six females, at least two of which were pregnant) (Table 1). One of the tagged bats could not be located on the day following tagging, and it is assumed that it either lost the tag or changed roost. To minimise biases that may result from bats being captured for tag attachment, the first night after attachment was excluded from the analysis. This resulted in the total of 86 nights of data. On average, for each tagged bat almost a week of data (6.73 days ± 3.58 SD; median 6 days, IQR 4 days) and 348.93 location fixes (±196.06 SD; median 304, IQR 136) were recorded.

5.1. Home range and foraging area

For all recorded fixes, a 15 m buffer was applied when calculating MCPs and cluster areas in order to account for the accuracy determined for three tags (mean 14.36 m ± 4.39 SD; median 10 m, IQR 14; 370 fixes). The analysis of utilisation distribution discontinuities indicated that on average the bats used 80% (±4.22 SD) cluster cores as presumed foraging areas. The remaining 20% would have caused a disproportionate increase in areas utilised by the bats, since it included the paths they used to travel to and from the feeding sites.

The area of the MCP for all tracked bats (Table 2) was 58 482 ha but individual home range areas (100% MCP) (Table 3) varied greatly among individuals (from 25 to 15 778 ha) with a mean of 5191 ha (±5667 SD) and median of 3554 ha (IQR 8741 ha). The total area of each bat's 80% cluster cores (Table 3) was considerably smaller than the home ranges (100% MCP) with a mean area of 87 ha (±125 SD) and median of 28 ha (IQR 119 ha), however considerable variation occurred among individuals (2–414 ha).

The plots of cumulative daily home range area (Fig. S1) indicated that out of 10 bats for which four or more days of data were recorded, only four showed a trend of home range area decelerating over the tracking period. The home ranges of all of the other bats showed a tendency to increase either in a linear or exponential fashion.

5.2. Habitat availability

The habitat within the entire home range of tracked colony (Table 2) was mainly composed of spiny forest (39.97%), sisal plantations (22.82%), agricultural land (17.40%) and degraded spiny forest (9.62%). The gallery forest formed only small percentage of the whole area (0.57%). However, the average of habitats available within each bat's home range (Table 2) was sisal (45.44% ± 24.21 SD), spiny forest (13.49% ± 11.98 SD), agricultural land (13.03% ±10.81 SD) and gallery forest (8.97% ± 14.93 SD).

5.3. Habitat preferences

Compositional analysis showed that habitats used by bats differed from their proportional availability (weighted mean Wilk's $\Lambda = 0.0002$, $X^2 = 128.4587$, df = 12, $P < 0.0001$, randomisation $p = 0.018$). The mean percentage of used habitat vs. available is summarised in Fig. 1.

The ranking matrix (Table 4) ordered habitat preferences from the most to the least selected. The preferences were as follows: overgrown sisal > gallery forest > sisal plantations >>> degraded gallery forest > fruit trees = water bodies > mixed forest > rice paddies = agricultural land > open areas > human settlement > degraded spiny forest > spiny forest,

Table 3
100% MCP and 80% cluster core home range areas (i.e. total area of all 80% cluster cores over the tagging period) for 15 GPS tagged *Pteropus rufus* bats in Berenty Reserve.

Bat ID	100% MCP area (ha)	80% cluster core area (ha)
24051	14688	314
24052	422	7
2406	9163	414
2407	646	6
24081	787	13
24082	13949	20
24091	45	2
24092	3929	172
2410	6968	67
24111	25	2
24112	3554	32
24113	5089	28
2412	15778	126
2413	217	5
2414	2599	96
Mean	**5191**	**87**
SD	**5667**	**125**
Median	**3554**	**28**
IQR	**8741**	**119**

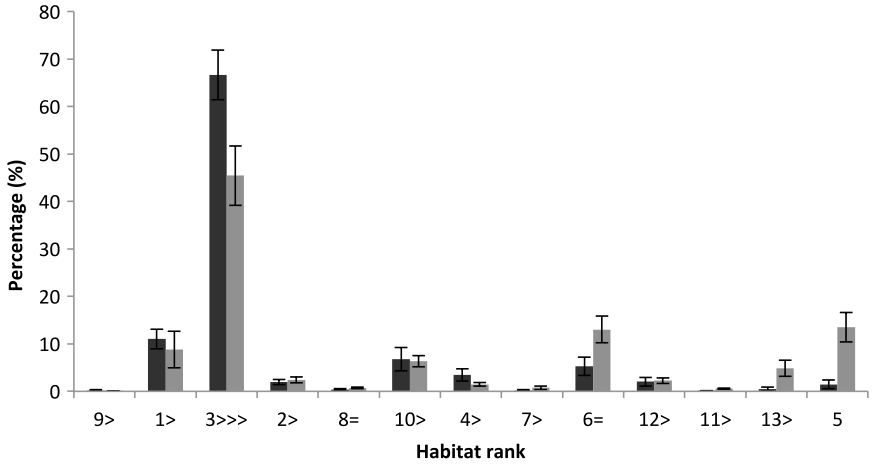

Fig. 1. Available habitat (100% MCP, grey bars) vs. used habitat (80% cluster, black bars) based on mean percentage area for all 15 tagged bats (bars represent SE). Habitat is ranked from the most selected (left) where '>' means selected over the adjacent habitat to the right with '>>>' indicating a significant difference compared with the following habitat in the ranking. Habitat codes: 1—gallery forest; 2—degraded gallery forest; 3—sisal plantations; 4—mixed forest; 5—spiny forest; 6—agricultural land; 7—rice paddies; 8—fruit trees; 9—overgrown sisal; 10—water bodies; 11—human settlement; 12—open areas; 13—degraded spiny forest.

where '>' means positively selected over the following habitat type, '>>>' significantly selected over the following habitat type and '=' equally selected to the following habitat type. When comparing all habitats, the sisal plantation and gallery forest were significantly selected over the other available habitats.

5.4. Foraging behaviour

The mean time at which bats emerged from the roost was 19.23 h (±32 min SD, $n = 15$) and the mean return time was 04.55 h (±51 min SD, $n = 15$). The study took place during the austral winter, when day length was increasing with sunrise at 06.21 h and sunset at 17.32 h on the 23rd of July. On the 10th of September, at the end of the GPS tracking study, sunrise was 05.50 h and sunset 17.44 h.

Spatial distribution of the individual home ranges (Fig. 2) indicated considerable overlap between each MCP, with an average overlap of 32.90% (±17.49 SD). The average of three bats with the smallest ranges (bat ID. 2406, 2410 and 24051) overlapped with almost every other bat, with an average of 85.1% (±23.39 SD), 70.03% (± 27.89 SD) and 64.17% (±28.63 SD) respectively. Their home ranges were confined to the gallery forest within which they roosted and a nearby sisal plantation, usually included within the larger home ranges of other bats. The core foraging sites vary in extent among the bats, however they demonstrate that bats are consistent in their use of feeding sites with little overlap between each bat's foraging areas (mean overlap was only 6.11% ±8.36 SD).

Table 4
The ranking matrix for habitat preferences (for each category on every row compared to corresponding habitat in each column) of all tracked *Pteropus rufus* bats. The matrix compares proportion of habitat within 80% clusters (used habitat) and 100% MCP (available habitat); + preference, − avoidance, a triple sign represents significant deviation from random at $P < 0.05$. The ranking list of all habitats ranges from 0 (least selected) to 12 (most selected).

	Gallery forest	Degraded gallery forest	Sisal plantation	Mixed forest	Spiny forest	Agricultural land	Rice paddies	Fruit trees	Overgrown sisal	Water bodies	Human settlement	Open areas	Degraded spiny forest	Rank
Gallery forest		+ + +	+	+ + +	+ + +	+ + +	+	+ + +	−	+ + +	+ + +	+ + +	+ + +	11
Degraded gallery forest	− − −		− − −	+	+ + +	+	+	+	−	+	+ + +	+	+	9
Sisal plantation	−	+ + +		+	+ + +	+ + +	+	+ + +	−	+ + +	+ + +	+ + +	+ + +	10
Mixed forest	− − −	−	−		+ + +	+	−	−	−	+	+	+	+ + +	6
Spiny forest	− − −	− − −	− − −	− − −		− − −	−	− − −	−	− − −	− − −	−	−	0
Agricultural land	− − −	−	− − −	−	+ + +		+	−	−	−	+	+	+	5
Rice paddies	−	−	−	+	+	−		−	−	−	+	+	+	5
Fruit trees	− − −	−	− − −	+	+ + +	+	+		−	−	+	+	+ + +	7
Overgrown sisal	+	+	+	+	+	+	+	+		+	+	+	+	12
Water bodies	− − −	−	− − −	−	+ + +	+	+	+	−		+	+	+	7
Human settlement	− − −	− − −	− − −	−	+ + +	−	−	−	−	−		−	+	2
Open areas	− − −	−	− − −	−	+	−	−	−	−	−	+		+	3
Degraded spiny forest	− − −	−	− − −	− − −	+	−	−	− − −	−	−	−	−		1

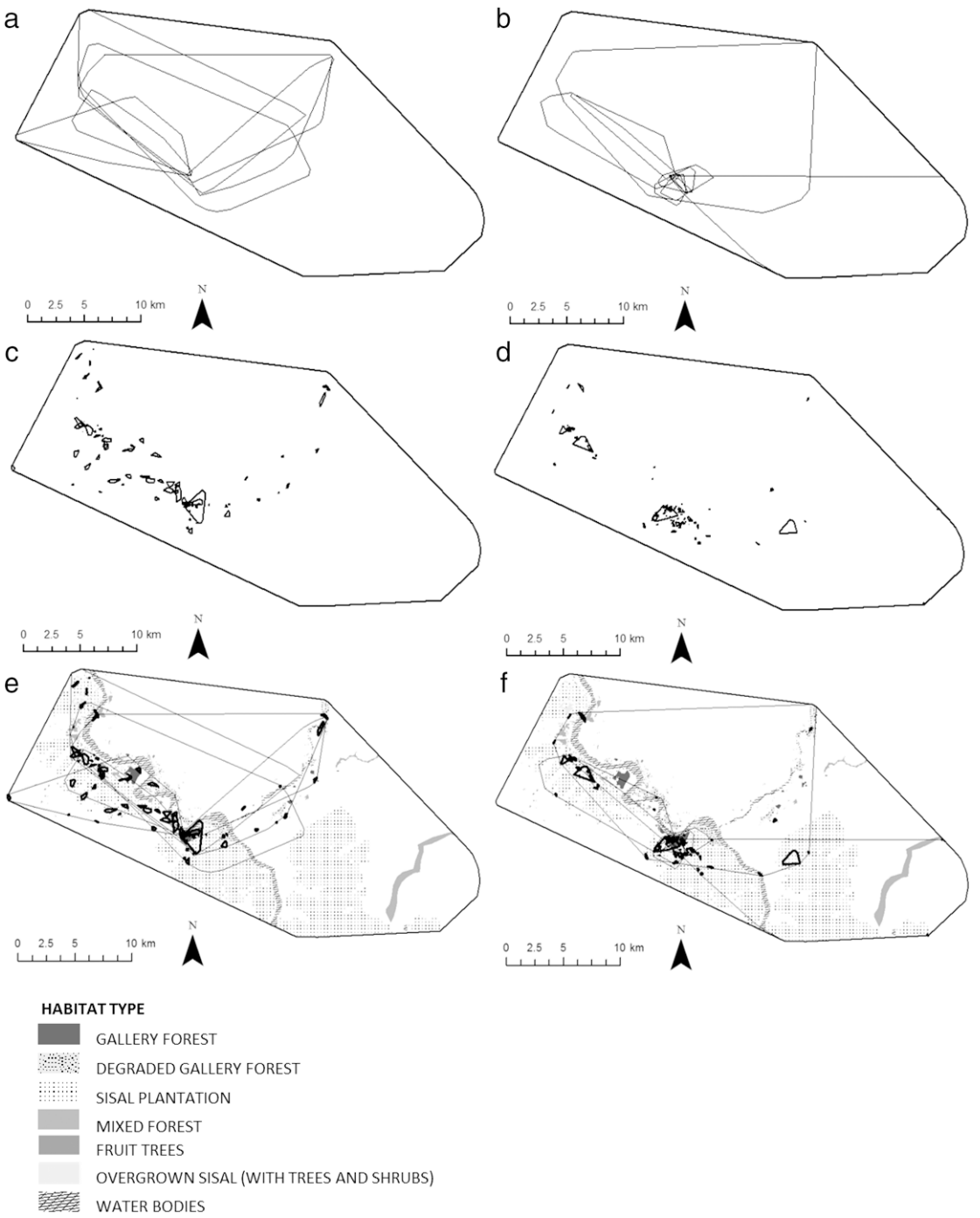

Fig. 2. Home range area of 15 tagged bats enclosing the individual 100% MCP home range areas of (a) females and (b) males; 80% cluster core foraging areas (c) females and (d) males and home ranges and cluster core foraging areas plotted on the map with most important habitat types highlighted (e) females and (f) males. Unshaded areas are predominantly spiny forest.

The home range and foraging area data were transformed to natural logarithms to obtain a normal distribution (Shapiro–Wilk test; 15 df, $P = 0.091$ and $P = 0.727$ respectively). An independent sample t-test showed that females had larger home range areas ($t = 2.924$, 13 df, $P = 0.015$) and foraging areas ($t = 3.432$, 13 df, $P = 0.005$) than male bats. The females' ($n = 6$) home range was on average 8175 ha (±5663 SD; median 6029 ha; IQR 11 364 ha) with a mean foraging area of 134 ha (±101 SD; median 111 ha; IQR 150 ha), while males' ($n = 9$) home range was 3201 ha (±5003 SD; median 646 ha; IQR 6227 ha) with a mean foraging area of 56 ha (±135 SD; median 7 ha; IQR 23).

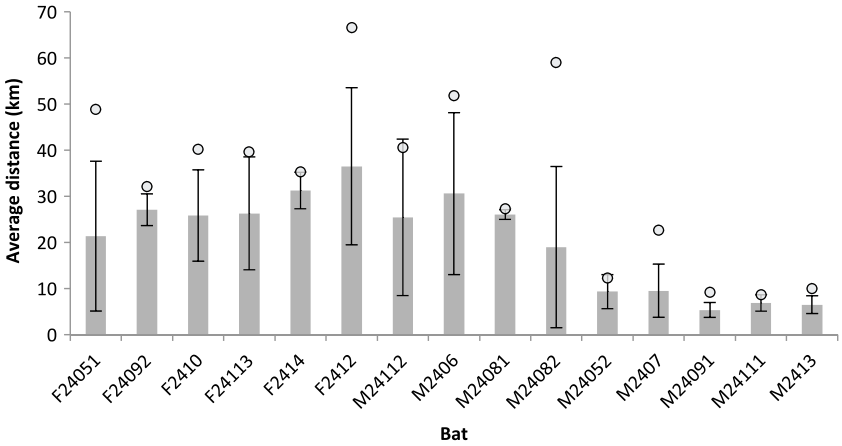

Fig. 3. Average nightly distances travelled by each bat (F—females and M—males) during the whole tracking period with the longest recorded distance indicated as a circle. Means and standard deviations illustrated.

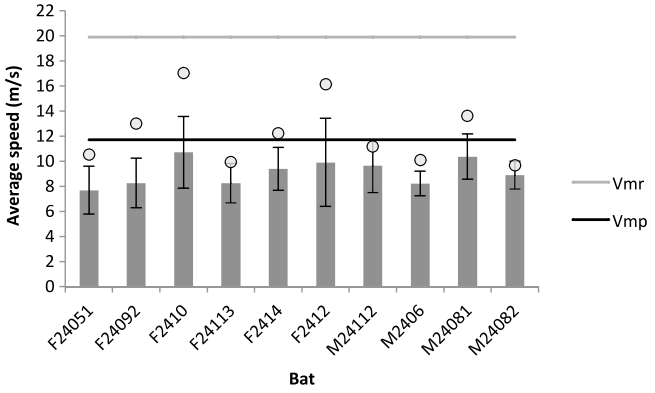

Fig. 4. Average speed of commuting flights for 10 bats (F—females and M—males). Circles indicate fastest recorded speeds for each bat and the lines indicate predicted minimum power flight speed (V_{mp}) and predicted maximum range flight speed (V_{mr}). Means and standard deviations illustrated.

5.5. Travelled distances and speed

Distances travelled by bats during one night of foraging varied greatly, with the shortest distance of 0.64 km recorded for a male and the longest of 66.55 km recorded for a female bat (Fig. 3). On average, females travelled 28.05 km (±5.2 SD; median 26.7 km; IQR 7.8 km) during a night's foraging while males travelled only 15.4 km (±9.89 SD; median 9.5 km; IQR 19.1 km). The distance travelled measured as a straight line from the roost to the most distant feeding site was on average 8.21 km (±7.92 SD; median 2.5 km; IQR 13 km) for males and 15.08 km (±2.31 SD; median 15.5 km; IQR 3 km) for females. An Independent sample t-test with unequal variances confirmed that females travelled greater distances than males ($t = 3.226$, 13 df, $P = 0.007$; Shapiro–Wilk test for normality 15 df, $P = 0.08$).

Reliable commuting flight speed data were obtained for 10 bats (Fig. 4). The speed of commuting flights between roosting and foraging areas was on average 9.13 m/s (±1.08 SD; median 8.6 m/s; IQR 0.83 m/s). The fastest speed was recorded for a female with an average of 17.04 m/s for a period during a non-stop flight lasting for 15 min.

The Pennycuick model (Fig. 5) predicted that most economical flight speed to minimise energy expenditure per time (minimum power speed, V_{mp}) for *P. rufus* would be of 11.7 m/s and at 20 m/s the energy expenditure would be most efficient to fly long distances (maximum range speed, V_{mr}).

6. Discussion

Our results show that *P. rufus* selects specific habitats for foraging, travels long distances during the night, and crosses open spaces regularly. The findings have implications for the ability of the bats to disperse seeds, and for their protection as they are often hunted as bushmeat (Jenkins and Racey, 2008; Oleksy et al., 2015).

6.1. Habitat preferences

The vegetation surrounding Berenty is composed mostly of sisal plantation, xerophytic scrubs, dense dry Didiereaceae (spiny) forest and savannah-like vegetation (Long and Racey, 2007). Indeed, the home range of the whole colony of *P. rufus*

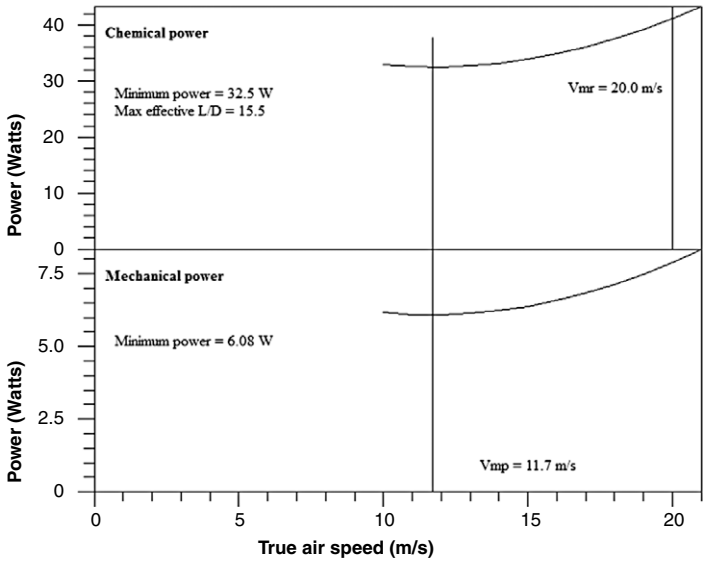

Fig. 5. Chemical (i.e. rate of energy consumption) and mechanical power (W) in relation to flight speed (m/s) predicted by the aerodynamic model of Pennycuick for *Pteropus rufus*. Predicted minimum power flight speed (V_{mp} m/s) and predicted maximum range flight speed (V_{mr}, m/s) were calculated based on the wing morphology of *P. rufus* and average body mass of the studied bats. L/D represents maximum effective lift-to-drag ratio when flying at the maximum range speed.

is dominated by spiny forest. This habitat type does not provide food resources for bats, thus they have to rely on sisal plantations and on small patches of gallery forest scattered along the river for feeding (Long and Racey, 2007).

Habitat ranking showed that *P. rufus* at Berenty prefer overgrown sisal plantations containing a mixture of shrubs, trees and sisal plants. Although this type of habitat is extremely limited in the area, it brings several advantages to the bats. Some native plants in unmanaged sisal plantation probably arrived as seeds dispersed by birds and bats and some were invaders from adjacent spiny forest, together with strips of Didiereaceae vegetation left in the plantation to protect the sisal from strong winds (Long and Racey, 2007). In all cases, the presence of other vegetation, especially trees, provides resting places and protection for the bats. Additionally, fruiting tamarind trees (*Tamarindus indica*) that are present in overgrown sisal plantations, and which sometimes also grow as single standing trees in human-managed plantations, provide food for the bats.

Gallery forest is the second most highly ranked habitat selected by the bats. This is the most natural and productive habitat available in the area and provides a roosting place for bats. The presence of tamarind trees and at least four large fig (*F. grevei*) trees in Berenty Reserve provide food resources during the dry season. Bats also visited several remnant forest patches in the area. These patches are usually highly fragmented due to timber extraction by local people as well as being degraded by cattle grazing (Long and Racey, 2007). However, bats probably promote seed exchange among the remnant forest fragments. In their review, Shanahan et al. (2001) indicate that among mammals, some bat species within the Pteropodidae are among the most important fig consumers. They contribute largely to a long-distance dispersal of fig seeds as well as to the recruitment of new trees in the forest and in isolated areas. Observations from the current study support this statement: the bats fed extensively on *F. grevei* over the time they were tracked and their seeds dominated all droppings (R. Oleksy, pers. obs.). Figs can be important pioneer species in forest regeneration (Goosem and Tucker, 1995; Kuaraksa and Elliott, 2013).

The sisal plantations at Berenty were selected in relation to their availability and thus are important for bats, especially as they cover an extensive area close to the main roost site. Although the inflorescences are generally pruned at an early stage to encourage harvestable vegetative growth, some plants escape this management practice and flowers are scattered throughout the plantations to provide an easily accessible and year-round food source for the bats. Foraging bats spend considerable time feeding on sisal nectar and pollen. The flowers produce pollen and nectar at night and have a strong musty smell that attracts bats (Long and Racey, 2007). Previous dietary analysis throughout the year showed that *P. rufus* from the Berenty area feed mainly on sisal pollen and nectar (56%) and tamarind fruits (39%) (Long and Racey, 2007). Results of the current study confirm that *P. rufus* bats at Berenty prefer to forage in habitats in which both these food sources grow in abundance.

Fruit trees are also important to bats as shown by the compositional analysis. They are usually planted as hedges that separate individual land patches and water bodies. Habitats with fruit trees are selected by bats to a similar extent as water bodies. This is perhaps because both habitats are usually adjacent to each other and bats may fly over water to reach a tree. The trees include commonly cultivated species such as mango, lychee and avocado, but tamarind trees and wild figs are probably most eaten. Agricultural land (maize, manioc, sweet potatoes) is ranked equally with open areas and bats often visited both habitats. However, the use of agricultural land is lower than expected, considering its availability. Agricultural land is largely treeless. However, although open areas did not provide food for bats, they regularly crossed them. Interest-

ingly, the exploitation of open areas was almost equal to what was expected from its availability. It is likely that bats feed on small patches of trees surrounded by or adjacent to open areas. For example, within the reserve, bats fed on *Eucalyptus* blossom adjacent to a grassy airstrip. Thus, bats fly over or feed near open areas in which they may disperse seeds that could provide important feeding patches in the future. Martin et al. (2009) found that activity and species richness in birds were higher in open areas in Madagascar where isolated trees were found, especially *Ficus* spp., when compared to areas with no trees. The visiting birds were mainly frugivores capable of dispersing seeds. This research results raises the possibility that bats may provide 'stepping stone' conditions for regeneration of forest, creating small patches of feeding habitat that might ultimately link or develop into more favourable habitat. Bats crossed cleared and agricultural (crop) fields frequently. Considering their ability to disperse seeds while flying, bats may be the key species responsible for the establishment of new trees in open areas as well as small forest patches. According to Martin et al. (2009), such isolated trees may attract frugivorous birds which would in turn enrich the soil seed bank by bringing in seeds from even more plant species. Similar suggestions were made by Cavallero et al. (2013) who proposed that remnant trees or artificial perches in burned or clear areas might favour passive restoration. Their study also indicated that, in similar areas, standing trees and perches are used by frugivorous birds, which increased rates of seed deposition. Furthermore, resulting seedlings and then fruiting trees attract more frugivores and facilitate seed flow between different communities at a landscape level (Cavallero et al., 2013).

Our results support the hypothesis that bats have the potential to promote seed dispersal within cleared and/or burned areas that they regularly cross. They also select habitats where their food is readily available. Additionally, they show preferences for small forest patches in which they disperse seeds.

6.2. Home ranges and foraging behaviour

The home range of all the tagged bats in the colony over 86 nights was almost 58,500 ha. Females had larger home ranges and core foraging areas than males. Females fed mostly away from the roosting sites and their foraging sites were more scattered across the range than those used by males. Males on the other hand preferred to feed in nearby sisal, close to the roosting site. The males used small home ranges presumably because their requirements were met within these ranges. Their fidelity to the feeding sites appeared more pronounced than in females. Bats with the largest home ranges foraged for food sources other than sisal, most likely figs as no other fruits were available to them during the study (apart from tamarind trees close to the roost site). Nonetheless, each of the bats fed to some extent on sisal every night, showing preferences for particular locations to which they returned regularly. During the bat netting on sisal plantations, it was observed that one to two bats per hour flew over the area. This suggests that the bats are widely dispersed over the plantation and their flight patterns do not interfere with each other. Wide dispersion is also supported by the general lack of overlap among the foraging areas of bats. However, this could be a consequence of tracking a relatively limited number of bats (15) out of over 600 present in the colony at the time of the study. The absence of overlap between home ranges and foraging areas also occurs in Egyptian fruit bats *Rousettus aegyptiacus* (Barclay and Jacobs, 2011). The majority of the tracked bats showed a trend for home range size to increase and their home range size did not reach an asymptotic value over the time they were tracked (Fig. S1). Therefore the home ranges described here are conservative, and bats would be likely to cover even larger areas over longer periods of time. The density of bats may affect their potential as efficient seed dispersers, as in *Pteropus tonganus* the dispersal of seeds too large for the bats to swallow becomes increasingly effective above a critical level of bat abundance (McConkey and Drake, 2006). In our study figs *Ficus* spp. were important components of the diet (Oleksy, 2014), and because the bats swallowed these small seeds, it is unclear whether a similar density-dependent effect would exist.

The study took place during the breeding season of *P. rufus*, when the females are expected to be pregnant. Although only two out of six tagged females showed obvious signs of pregnancy, it is possible that those females with body mass of 700 g and over were in the early stages of pregnancy. Gestation may explain the difference in feeding behaviour between males and females. Both pregnancy and lactation increase demands for energy and nutrients in females, which in turn may influence their foraging strategy (Barclay, 1989). Calcium becomes a crucial resource during pregnancy and lactation for the development of the skeletal system of embryos and pups (Barclay, 1994). However, diets consisting of fruit and nectar are generally low in calcium (Barclay, 1994). Barclay (2002) tested the hypothesis that nectar of flowers that were visited by flying foxes in Queensland, Australia, provided high calcium content as a reward for pollination. After testing 22 species of plants, he concluded that although there was a higher concentration of calcium in the nectar of flowers visited by bats, the concentration was still unlikely to fulfil the needs of gestating and lactating females. Rather, visiting such flowers reduces the amount of calcium that bats need to obtain from other sources (Barclay, 2002).

The sisal plantation in Berenty offers easy foraging for bats by providing abundant nectar and pollen. Although pollen is high in proteins (Law, 1992), it contains low calcium levels (Stanley and Linskens, 1974). Therefore, females must search for other sources of calcium, the most likely being figs (O'Brien et al., 1998). It is therefore very likely that female *P. rufus* had much larger home ranges because they tend to search for figs. Furthermore, foraging bats often fed along the rivers where fig trees, especially *F. grevei*, are likely to be found (Dalecky et al., 2003).

In their study on *Rousettus aegyptiacus*, Barclay and Jacobs (2011) predicted that during reproduction females should be more selective in their diet and search for figs. Females should also forage for longer than males in order to meet their nutritional requirements. All of these were assumed to increase the size of female home ranges. However, Barclay and Jacobs (2011) found that both sexes had similar home ranges with the only difference that females tended to forage more often in native forest patches than males. No difference in home range size between sexes occurs in *Dobsonia minor* in Papua New

Guinea. However, the core foraging areas were larger in female bats. This could reflect greater nutritional requirements of females linked to reproduction (Bonaccorso et al., 2002). Such findings are similar to the behaviour of *P. rufus* females in our study, which had greater core foraging areas than males.

Pteropus rufus often showed great fidelity to their feeding sites, suggesting that the bats generally concentrate on spatio-temporal predictability to minimise the energetic costs of commuting and searching for food (Fleming and Heithaus, 1986). Such behaviour seems to be relatively common in a range of nectarivorous and insectivorous bat species (e.g. Heithaus and Fleming, 1978, Kerth et al., 2001 and Weber et al., 2009).

6.3. Travel distances and flight speed

Flying foxes are known to travel long distances, often within more than 10 km from their roost to the feeding sites (Corlett, 2009). However, the distances vary depending on species and their habitat—*P. alecto* travelled between 5–20 km a night (Palmer and Woinarski, 1999; Marcus and Hall, 2004) and *P. poliocephalus* 17–25 km (Spencer et al., 1991). The same species showed a median displacement distance of 821 km over 30 weeks in a satellite telemetry study (Roberts et al., 2012). In mainland Africa, *Eidolon helvum* foraged 59 km away from the roosting site in a single evening (Richter and Cumming, 2008). In American Samoa, *P. tonganus* flew between 5 and 23 km during foraging, with the maximum-recorded distance of 46.7 km (Banack and Grant, 2002), while in Malaysia the maximum foraging distance for *P. vampyrus* was over 87 km (Epstein et al., 2009). The results of our study conform to the general view that pteropodids make long distance movements to feed, with average total foraging distances of 28 km for female *P. rufus* and 15 km for males. These distances must be viewed as conservative, as home ranges did not reach asymptotic values over the time that bats were tracked.

Our study also indicates that female bats fly longer distances while foraging than males, which was expected considering their large home ranges. However, the differences between sexes must be treated with caution given that more males were tracked than females, and the relatively small sample sizes and short tracking periods. Nevertheless, similar results were found for *P. alecto* (Palmer and Woinarski, 1999). Bonaccorso et al. (2002) also suggest that female *Dobsonia minor* may have longer commuting flights between roosting and feeding areas.

McWilliam (1985) reported that smaller, less dominant flying foxes travel longer distances than larger, more dominant individuals. This was supported by Banack and Grant (2002) who found *P. tonganus* juvenile males travel on long, so called 'exploratory flights'. In our study, two adult male *P. rufus* had exceptionally larger home ranges and thus longer nightly foraging distances than other males. For example, bat number 2406 travelled long distances on two nights out of four while bat 24 082 on only one night out of seven. These long distance movements may involve exploration for new food resources.

The average speed of commuting flights for *P. rufus* was about 9 m/s with the fastest recorded flight of over 17 m/s. According to Pennycuick's model, the optimum speed for *P. rufus* (V_{mp}) would be nearly 12 m/s to minimise the use of energy or 20 m/s to maximise flight range (V_{mr}). It has been predicted that bats would fly faster than V_{mr} when commuting to their feeding sites to maximise their foraging time, especially when prey availability decreases over time (Britton et al., 1997). However, the average speed of *P. rufus* is well below V_{mr} and slightly less than V_{mp}. Although *P. rufus* is reported to soar, all flight speeds reported here were made at night when thermal convection currents are absent. During the day, the bats are often seen to soar around the roosting site or towards the alternative roosting place when disturbed by people (pers. obs.). However, the species is also known to glide extensively (Norberg et al., 2000). Indeed, Norberg et al. (2000) calculated a minimum sinking speed for *P. rufus* close to 9 m/s, and a best glide speed of 10 m/s. It is therefore possible that the flight speeds reported here are at least in part being used to optimise gliding performance.

It is also important to note that the flight speed measurements reflect ground speeds, rather than air speeds, as wind speeds could not be measured reliably. Straw-coloured fruit bats *Eidolon helvum* decrease airspeed in tailwinds to maintain an almost constant groundspeed (Sapir et al., 2014). However, during the fieldwork, most nights were calm. Wind speeds affect airspeed (Pennycuick, 1997, 2001) and groundspeeds should not be used in determining how closely animals fly to predicted 'optimal' speeds. Nevertheless, the speeds reported here were relatively consistent across 10 individuals and are likely to be relatively accurate estimates of average airspeeds given this consistency across a wide range of conditions.

Pteropus poliocephalus is of similar size to *P. rufus* and metabolic measurements from bats in wind tunnels suggest that this species may not fly at V_{mr} because flight endurance is compromised at that speed: indeed flight range may be maximised at V_{mp} (Carpenter, 1985). It may therefore be possible that large pteropodids are unable to use V_{mr} for sustained flight (Norberg and Rayner, 1987).

Previous studies recorded similar speeds for commuting flights of flying foxes to those recorded here (*P. vampyrus* 18 m/s Epstein et al., 2009); *P. dasymallus* 7–11 m/s (Nakamoto et al., 2009); *P. poliocephalus* up to 18 m/s (Carpenter, 1985) and *P. alecto* 10 m/s (Thomas, 1975). Speeds of over 7 m/s were recorded for *E. helvum, Hypsignathus monstrosus* and *R. aegyptiacus* in a wind tunnel Carpenter (1986). GPS tracking of *Eidolon helvum* revealed median groundspeeds close to 11 m/s, and a median airspeed of around 9 m/s (Sapir et al., 2014). Tidemann and Nelson (2004) suggested that high speeds of flying *P. poliocephalus* are wind-facilitated. Indeed, many flying foxes are known to reduce energy consumption in flight by soaring and gliding and *P. rufus* is listed among them (Norberg, 1990; Norberg et al., 2000).

The findings of this study reject the hypothesis that *P. rufus* would fly at V_{mr} to maximise its foraging time. Instead, it suggests that these bats use more cost-effective methods of travel perhaps to maximise endurance, and/or to improve gliding performance.

7. Conclusion

We present new information regarding the feeding and ranging behaviour of *P. rufus*, and confirm that the species has the potential to disperse seeds over long distances and contribute to forest regeneration at a large scale. Long-distance movements over a wide range of sites are likely to be beneficial for seed dispersal as each bat potentially creates individual seed shadows along its travelling route. Ranking of the habitat used by bats indicates their ability to travel within cleared areas, making these animals important contributors to forest regeneration. All the bats tracked fed on sisal, the pollen of which provided an important source of protein. However, there was a strong preference for native forest remnants, indicating that despite its scarcity, this habitat still remains of high importance to *P. rufus*. Given that bats can fly over 10 km to their feeding sites, they should be protected (e.g. from hunting) in an area of at least 400 km^2 around the roost site.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2015.02.012.

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